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Diversity, morphological phylogeny, and distribution of bats of the genus *Molossus* E. Geoffroy, 1805 (Chiroptera, Molossidae) in Brazil

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**ABSTRACT**

Tenuous descriptions of many species and subspecies of mastiff bats make the taxonomy of *Molossus* E. Geoffroy, 1805 confusing and unstable. *Molossus* is one of the most diverse genera of free tailed bats in the pantropical family Molossidae Gervais, 1856. Given their impressive variation due to geography, sex, and ontogeny, and incomplete knowledge about species boundaries, a comprehensive taxonomic revision of the genus is needed. In addition, the level of genetic divergence, even among morphologically well-characterized species is low, often making diagnosis of groups difficult and likely resulting in an underestimation of the number of species. Brazil has a wide territory harboring many different physiognomies, but with no study focusing on the morphological variation and taxonomy of *Molossus* available. Therefore, we have analyzed qualitative and quantitative characters from 493 specimens belonging to nine species of *Molossus*, and conducted a wide comparative morphological analysis of the species occurring in Brazil. In addition, we propose a hypothesis of phylogenetic relationships within *Molossus* based on morphology, establishing the morphological characters for diagnosis and identification of species, and update the geographic distribution of *Molossus* species in Brazil, with range extensions for four taxa. Six species, *Molossus rufus* E. Geoffroy, 1805, *Molossus molossus* (Pallas, 1776), *Molossus coibensis* Allen, 1904, *Molossus aztecus* Saussure, 1860, *Molossus currentium* Thomas, 1901, and *Molossus pretiosus* Miller, 1902 occur in Brazil. We bring support for the synonymy of *Molossus bondae* Allen, 1904 with *M. currentium*, as suggested by several authors.
Molossidae Gervais, 1856 represent the fourth most diverse subspecies to the genus. In the most influential review of while Goodwin (1956, 1959) added one species and one (1989), but its taxonomy has been in a state of constant flux, et al. (2016). However, several morphological and physiological characteristics vary among geographic regions (Davison & Wilkison 2002), and only part of this variation has been analyzed (Willig 1983; Dolan 1989; Jennings et al. 2000; López-González & Presley 2001; Souza 2011; Gregorin et al. 2011; Catzeflis et al. 2016).

Molossus has been reviewed by Miller (1913) and Dolan (1989), but its taxonomy has been in a state of constant flux, and the actual number of species is not a consensus among authors. For example, Miller (1913) recognized 18 species while Goodwin (1956, 1959) added one species and one subspecies to the genus. In the most influential review of Molossus, Dolan (1989) recognized seven species: Molossus molossus (Pallas, 1776), Molossus azteca Saussure, 1860, Molossus currentium Thomas, 1901 and Molossus pretiosus Miller, are present in Brazil. Our data confirm the synonymy of Molossus bondae Allen, 1904 with M. currentium, suggested by several authors.
Grande do Sul, encompassing a wide latitudinal range. *Molossus* is also commonly found in urban areas and in houses, making it one of the most frequently observed free-tailed bats in Brazil. Six species of *Molossus* are currently recognized for the country (Dolan 1989; Gregorin & Taddei 2000; López-González & Presley 2001; Gregorin et al. 2011), but the diversity of *Molossus* was historically underestimated, with only two species being recognized for a long time: the small-sized *M. molossus* and the larger *M. rufus* (synonym of *M. ater*). Dolan (1989) recorded *M. coibensis* as occurring in the state of Mato Grosso (under the name *M. cherriei* Allen, 1916); however, this record was not mentioned by subsequent authors (e.g. Gregorin & Taddei 2002). In the 2000's, some publications improved our knowledge about *Molossus* in Brazil, with the addition of four species recognized for the country: *M. pretiosus* (Gregorin & Taddei 2000; Nogueira et al. 2008), *M. currentium* (López-González & Presley 2001; Tavares et al. 2010; Bernard et al. 2011), *M. aztecus* (Gregorin et al. 2011), and *M. coibensis* (Dolan 1989; Costa et al. 2013).

Therefore, due to the presence of many species of *Molossus* in Brazil, the high phenotypical variation in some species, such as in *M. molossus* (Souza 2011) and to the uncertainties that surround its taxonomy in the large and ecologically diverse Brazilian territory, an overview of the taxon is necessary to determine the number of species of *Molossus* currently present in Brazil, establishing morphological diagnostic traits and defining the limits of their geographical range. It can be expected that the hidden taxonomic diversity found in Brazilian *Molossus* will occur in other ecological, geological and environmental complexes countries such as Peru, Ecuador, and Colombia. In addition, *Molossus* has been divided into two morphogroups based on several morphological traits such as banding pattern in the dorsal hairs and cranio-dental morphology (Dolan 1989; Gregorin et al. 2011). However, there are no studies addressing the relationships within *Molossus* using a cladistic approach neither discussing the diagnosis of species-group based on a cladistic view (e.g. apomorphies). Therefore, this study aims at: 1) making a comparative morphological analysis of the species within *Molossus* from Brazil; 2) establishing morphological characters for definition and identification of species based mainly in apomorphic states of characters as recovered by phylogeny; and 3) updating the geographic distribution of several species of *Molossus* in Brazil.

**MATERIAL AND METHODS**

**EXAMINED MATERIAL**
We examined 493 specimens from nine species of *Molossus* including nine *M. bondae* from Colombia, 26 *M. coibensis* (including three individuals previously identified as *M. barnesi*) from Brazil, Panama, French Guiana, and Guatemala), 255 *M. molossus* (mainly from several Brazilian localities), 59 *M. aztecus* (from Mexico and Brazil), 11 *M. currentium* (from Colombia, Brazil, and Panama), 32 *M. pretiosus* (from some Mexico, Brazil, and Venezuela), 80 *M. rufus* (mainly from several Brazilian localities), 10 *M. sinaloae* (from Central America) and a single indeterminate specimen of *Molossus* sp. from Brazilian Caatinga, state of Bahia, Northeastern Brazil (possibly a new taxon). Additionally we have also examined six specimens of *Promops centralis* Thomas, 1915 and seven of *Eumops auripendulus* Shaw, 1800 to use as outgroup in the phylogenetic analysis. The choice of these species was based on the phylogeny proposed by Ammerman et al. (2012) and Gregorin & Cirranello (2016). The specimens were initially identified based on the taxonomic identification keys of Gregorin & Taddei (2002) and Eger (2008), and on the characteristics described by Dolan (1989) and Gregorin et al. (2011). Only adults, defined as having all cranial sutures closed and complete epiphysal ossification of metacarpal and phalanx, of both sexes were examined. We have also analyzed the holotypes of *M. coibensis* (AMNH 18731), *M. bondae* (AMNH 23661), *M. sinaloae* (AMNH 24524), *M. molossus verrilli* Allen, 1908 (AMNH 25764), and *M. pretiosus* (USNM 102761), and photographs of the holotype of *M. rufus* (MNHN-ZM-MO-1997-1847). In addition, toptotypes of *M. alvarezi*, *Molossus molossus milleri* Johnson, 1952, *M. molossus*, and *Molossus molossus pygmaeus* Miller, 1900 were also included in our study. *M. aztecus* was originally described for Amecameca, Mexico (Saussure, 1860). Although we did not include in our sampling toptotypes of this species, we have examined *M. aztecus* from the state of Oaxaca and Colima in Mexico (Appendix 1), which are located in south and northwestern from Tlaxaca respectively, engulfing the geographic distribution of this taxa. The list of the analyzed specimens, their geographic locations and institutions in which they are deposited are presented in Appendix 1.

**MORPHOLOGICAL ANALYSIS**
Qualitative characters included those from external, cranial and dental morphology. The morphometric analyses included one external and 12 cranial variables, all taken using digital calipers with 0.01 mm of accuracy (Giannini & Simmons 2005; Tavares 2008; Fracasso et al. 2011). The measurements were: Forearm length (FA); Greater length of skull with incisors (GSLI); Greater length of skull excluding incisors (GSL); Braincase width (BCW); Condyl-o-incisor length (CIL); Zygomatic breadth (ZB); Palatal length (PAL); Width across upper molars (M-M); Width across upper canines (C-C); Width across upper incisors (I-I); Length of maxillary toothrow (C-M); Height of the sagittal crest (SAR); and Interorbital width (IOW) (Fig. 1).

**DATA ANALYSIS**
A Student t-test was carried out to test for sexual differences within each species. Because not all variables were normally distributed, the data were log-transformed prior to the analysis. Significant sexual differences were observed for all species (P<0.05) and, therefore, males and females were treated separately in subsequent analyses. A Principal Component Analysis (PCA) was carried out using the correlation matrix for 13 variables and a Multiple Analysis of Variance (MANOVA) was performed based on the same set of characters to test if there were significant differences among species.
The pattern of morphology within species can vary due to environmental conditions, which are differentiated along the latitudinal gradient (Brown 1995; Ashton et al. 2000; Salewski & Watt 2017). In Brazil, several environmental variables, such as temperature and humidity, vary greatly between north and south (Souza 2011). Therefore, a multiple regression analysis within species was conducted to verify the relationship between latitude and body size. Only *M. molossus*, *M. aztecus*, and *M. rufus* were analyzed because only these species had enough individuals and localities to provide robust analyses (see Appendix 1). PCA and MANOVA within each of these species were also used to verify the differences among populations at different latitudes. Missing data (due to damaged skulls) were estimated using the algorithm “estimation-maximization” (Little & Rubin 1987) for skulls with a maximum 20% of missing data. The significance level for all statistical tests was $P = 0.05$. Statistical analyses were performed using Systat 11, R 3.1.0 (R Core Team 2005) and Past 2.17 (Hammer et al. 2001).

**Geographical distribution**

For estimation of geographic distribution of *Molossus* species in Brazil only material with voucher specimens was considered. The maps were built in Quantum Gis 2.0.1 (QGIS Development Team 2009).
**Phylogenetic Analysis**

A total of 40 morphological characters were coded, of which 13 are new characters for phylogenetic relationships within bats, and 27 represent modified versions from previous papers (Wetterer et al. 2000; Tavares 2008; Gregorin 2009) (Fig. 2; Appendix 2). The characters were equally weighted and multi-state characters were treated as unordered. A parsimony analysis was performed in the Tree analysis using New Technology (TNT) program (Goloboff et al. 2008) using implicit enumeration to evaluate the congruence among morphological characters (Hennig 1966; Farris 1983). The definition of character states and coding were based on the outgroup method (Farris 1983; Nixon & Carpenter 1993). Tree statistics, including consistency index (CI) and retention index (RI), were also calculated using TNT. Clade stability was assessed using bootstrap analysis (Felsenstein 1985), conducted with 5000 replicates, and Bremer support (Bremer 1994).

**Identification Key**

An identification key was elaborated based on the characters obtained for the phylogenetic reconstruction and on the morphological comparisons used to identify and differentiate species of *Molossus*. We highlight that the identification key does not reflect the phylogeny, but each entry contains a set of both derived and plesiomorphic characters, that just permits the accurate identification of taxa.

**Results**

**Qualitative Characters**

A set of external, cranial, and dental characters (Figs 1; 2) allowed us to recognize at least six morphologically well-defined species of *Molossus* occurring in Brazil (*M. coibensis*, *M. molossus*, *M. aztecus*, *M. currentium*, *M. pretiosus*, and *M. rufus*), and a putative new species from Caatinga. Based on morphological similarity, we can cluster these species in three phenetic groups: (*M. aztecus* + *M. coibensis* + *M. rufus*); (*M. molossus* + *M. currentium*); and (*M. pretiosus*). *Molossus sinaloae* does not occur in Brazil and it was not included in this species account.

The group composed of *M. aztecus*, *M. coibensis*, and *M. rufus* has monochromous dorsal hairs or with a basal band slightly paler and not covering more than 1/5 of the hair, and the pelage is usually dark or blackish. The skull is robust with short and inflated rostrum and a broad braincase (Fig. 2B). The sagittal and lambdoidal crests are well developed and the occipital complex is square-shaped (Fig. 2F). Dental variation is restricted to upper incisors for all species of the genus, as noted by Dolan (1989) and Gregorin & Taddei (2000). The upper incisors are spatulate with pincer-like and convergent tips (Fig. 2H) and do not project beyond the canines in lateral view (Fig. 2A). However, the body and skull dimensions of these species are very different. *M. coibensis* is the smallest species of *Molossus*, followed by *M. aztecus* with an intermediate size within the group, and *M. rufus*, which is the largest species of the genus (Table 1). In addition, some characteristics of the skull also differ among these taxa. The infraorbital foramen in *M. coibensis* opens frontally in rostral view (Fig. 2G), and the rostrum is more robust (Fig. 2G), whereas, in *M. aztecus* and *M. rufus* the infraorbital foramen opens laterally (Fig. 2H), while the rostrum is triangular and more gracile (Fig. 2E). The basisphenoid pits are very shallow or absent in *M. coibensis* (Fig. 2C) and of moderate depth in the other two species (Fig. 2D). In addition, the mastoid process is directed towards the foramen magnum in *M. rufus* (Fig. 2F), and ventrally directed in *M. coibensis* and *M. aztecus* (Fig. 2E).

The group composed of *M. currentium* and *M. molossus* has marked bicoloured cocoa to cinnamon brown dorsal hairs with a whitish basal band reaching 1/2 to 1/4 of the total length of the hair. However, *M. currentium* tends to have a shorter band than *M. molossus*. In these species, the skull is more elongated (Fig. 2A) and the upper incisors are long and tapered (Fig. 2G). In addition, the basisphenoid pits are moderate in depth (Fig. 2B), and the mastoid process is directed ventrally (Fig. 2E). Despite some overlap in measurements between *M. molossus* and *M. currentium*, the latter tends to have larger external and cranial measurements than *M. molossus* (Table 1). These species also differ in qualitative cranial characters: *M. currentium* has the infraorbital foramen directed laterally (Fig. 2H) and very well developed sagittal and lambdoidal crests (Fig. 2F, B), whereas *M. molossus* has the infraorbital foramen directed frontally (Fig. 2G) and undeveloped sagittal and lambdoidal crests (Fig. 2A, E).

*M. pretiosus* is unique within the genus, with many characters showing an intermediate state between both previous groups. *M. pretiosus* overlaps *M. currentium* and *M. rufus* in forearm and cranial measurements. However, in general it is slightly larger than *M. currentium* and smaller than *M. rufus* (Table 1). In *M. pretiosus* the upper incisors are thin and elongated, but often they are convergent at the tips and project beyond the canines, an intermediate condition when compared to other species of the genus. *M. pretiosus* also has an evident crest between the basisphenoid and basioccipital pits, due to the very deep basisphenoid pits, which also differentiates this species from other *Molossus*.

**Morphometric Variation**

One external and 12 cranial variables were measured from six recognized species of *Molossus* and from one undetermined individual from the Brazilian Caatinga (*Molossus sp.*) (Table 1). Males are statistically larger than females with different variables showing significant differences in each species. Most of the species have males with larger GLSI, GSL, SAR, and ZB (Table 2). Additionally, some qualitative characters, such as the development of sagittal and lambdoidal crests are sexually dimorphic. Therefore, males and females were treated separately in subsequent analyses.

The interspecific variation indicated by the PCA was similar for males and females (Fig. 3). Two main groups, distinguished by size, were evident in analyses of both sexes.
One group is formed by larger individuals representing *M. pretiosus*, *M. sinaloae*, and *M. rufus*, while the other one is composed of individuals of small to medium size representing *M. currentium*, *M. aztecus*, *M. molossus*, and *M. coibensis*. For the females, *Molossus* sp. is placed between the two groups in the PCA (Fig. 3). The first two principal components explain 84.81% of the total variation in males and 86.99% in females (Table 3). The MANOVA corroborates the PCA and shows significant differences among species for both males (P < 0.001, F = 56.70) and females (P < 0.001, F = 47.50).

### Table 1

Measurements in mm of species of *Molossus* E. Geoffroy, 1805 occurring in Brazil. *Molossus* sp. refers to the putative new species capture in the Brazilian Caatinga. Abbreviations: see Material & Methods.

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<th>Species</th>
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<td><em>M. aztecus</em> Saussure, 1860</td>
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One group is formed by larger individuals representing *M. pretiosus*, *M. sinaloae*, and *M. rufus*, while the other one is composed of individuals of small to medium size representing *M. currentium*, *M. aztecus*, *M. molossus*, and *M. coibensis*. For the females, *Molossus* sp. is placed between the two groups in the PCA (Fig. 3). The first two principal components explain 84.81% of the total variation in males and 86.99% in females (Table 3). The MANOVA corroborates the PCA and shows significant differences among species for both males (P < 0.001, F = 56.70) and females (P < 0.001, F = 47.50).
Multiple regression analysis revealed that the samples from lower latitudes have smaller body and cranial sizes than populations at higher latitudes in *M. molossus*. In males, the measurements GLS, CI, I-I, and FA showed a high correlation with latitude ($P < 0.001$). In contrast, the variables correlated in females were GLS ($P = 0.003$), ZB ($P = 0.001$), SAR ($P = 0.003$), and FA ($P = 0.008$). In males of *M. aztecus* GLS ($P < 0.001$) was the only variable correlated with latitude. However, this relationship in females is supported by ZB ($p = 0.009$) and SAR ($P = 0.042$).
Males of *M. rufus* only have I-I (P = 0.043) associated with the latitude, while the females showed a differentiation in IOW (P = 0.015), PAL (P = 0.040), M-M (P = 0.006), and SAR (p = 0.006).

The PCAs carried out within each species of *Molossus* shows no differentiation among samples, except for a male sampling of *M. molossus* from southern Brazil (Fig. 4; Table 4). This sample grouped separately and showed larger body and cranial measurements than other individuals. PC1 and PC2 explain 90% of the total variation and are both driven by size (Table 4). The ANOVA confirms that the samples from southern Brazil are morphometrically

![Figure 3](image1.png)

![Figure 4](image2.png)

Table 2. — P-values of t-test of measurements between male and female *Molossus*. Abbreviations: see Material & Methods.

<table>
<thead>
<tr>
<th>Variables</th>
<th><em>M. coibensis</em> (Miller, 1902)</th>
<th><em>M. molossus</em> (Pallas, 1766)</th>
<th><em>M. aztecs</em> Saussure, 1860</th>
<th><em>M. currentium</em> Thomas, 1901</th>
<th><em>M. pretiosus</em> Miller, 1902</th>
<th><em>M. rufus</em> (E. Geoffroy, 1805)</th>
</tr>
</thead>
<tbody>
<tr>
<td>GSLI</td>
<td>0.014</td>
<td>0.637</td>
<td>0.013</td>
<td>0.000</td>
<td>0.005</td>
<td>0.000</td>
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<tr>
<td>GSL</td>
<td>0.011</td>
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<tr>
<td>CM</td>
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<tr>
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<td>0.001</td>
</tr>
<tr>
<td>C-C</td>
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</tr>
<tr>
<td>I-I</td>
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<td>0.100</td>
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<tr>
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<tr>
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<tr>
<td>SAR</td>
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<tr>
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distinct from other groups previously identified as *M. molossus* (*P* < 0.01; *F* = 0.6). In the MANOVA, the effect of variation among samples is highly significant for males of *M. molossus* (*P* = 0.001), but not significant for females of *M. molossus*, *M. aztecus*, and *M. rufus* (*P* > 0.6), consistent with the PCA.

**Table 3.** — Eigenvalue and PCA loading for the first and second components. Abbreviations: see Material & Methods.

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
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<td>Females</td>
</tr>
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<td>C-M</td>
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<td>GSL</td>
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<tr>
<td>BCW</td>
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<tr>
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<tr>
<td>C-C</td>
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<tr>
<td>M-M</td>
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<tr>
<td>ZB</td>
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<td>0.28</td>
</tr>
<tr>
<td>PAL</td>
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<td>0.30</td>
</tr>
<tr>
<td>FA</td>
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</table>

**Table 4.** — Eigenvalue and PCA loading for the first and second components in *M. molossus*. Abbreviations: see Material & Methods.

<table>
<thead>
<tr>
<th></th>
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<tbody>
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<td>I-I</td>
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<td>C-M</td>
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<td>0.20</td>
</tr>
<tr>
<td>GSL</td>
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<td>BCW</td>
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<tr>
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<td>0.36</td>
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</table>

**Phylogeny**

 Parsimony analysis resulted in eight most parsimonious trees with 56 steps each (CI = 0.84; RI = 0.83). A strong support (Bootstrap = 100% and Bremer = 10) was found for *Promops* as the sister group to *Molossus*, instead of *Eumops*, and for the monophyly of *Molossus*. The consensus tree (Fig. 5) shows
low support for the relationships within Molossus. However, the clade composed of M. coibensis + M. rufus + M. pretiosus + M. currentium + M. aztecus is divergent from the clade M. molossus + M. sinaloae. In addition, the individual from Caatinga (Molossus sp.) does not occupy a defined position within the genus and we consider it as a soft polytomy in the consensus tree (Coddington & Scharff 1996). Based on this phylogenetic hypothesis, synapomorphies of Molossus include incisors with convergent tips or ventrally directed (character 10, states 1 and 2), one upper premolar (c. 11), a reduced third lower premolar (c. 12), and a domed occipital complex (c. 18). The clade composed by M. coibensis + M. currentium + M. aztecus + M. pretiosus + M. rufus is supported by pincer-like incisors (c. 10, state 1), quadrangular occipital complex (c. 38, state 1), and well developed lambdoidal and sagittal crests (c. 36, state 2 and c. 37, state 1). The clade M. molossus and M. sinaloae is supported by triangular occipital complex (c. 38, state 0), thin and elongated incisors (c. 10, state 2) and low sagittal crest (c. 36, state 1) (see Appendix 2). These two branches reflect partially the previous phenetic grouping of species (Dolan 1989). A third lineage is composed solely by Molossus sp and this branch is defined by characters such as low sagittal crest, triangular occipital complex, thin and elongated incisors, moderate occipital pits.

SYSTEMATICS

Family Molosauridae Gervais, 1856
Genus Molossus E. Geoffroy, 1805

Molossus aztecus Saussure, 1860


Emended Diagnosis. — Medium-sized Molossus with dense and long dark dorsal fur. Dorsal hair reaching 6.0 mm and varying from dark cocoa brown to blackish. Monochromatic dorsal hairs or with a small pale basal band covering no more than ¼ of the total length. Forearm length averages 39.5 mm in males (35.9–41.5) and 39.0 mm in females (35.0–41.9). Greatest length of skull averages 17.6 mm (16.3–18.3) in males and 16.7 mm (16.1–18.6) in females (Table 1). Basioccipital pits moderate in depth (Fig. 6A). Occipital complex rectangular in posterior view due to the development and inclination of the lambdoidal crests (Fig. 6B). Inflated rostrum and rounded braincase (Fig. 6C). infraorbital foramen opening laterally in frontal view (Fig. 6D). Nasal process of the premaxilla well developed in males, protruding over the nasal cavity (Fig. 6C). Skull with mastoid processes oriented ventrally in posterior view. Triangular rostrum in frontal view with narrow dorsal portion (Fig. 6D). Upper incisors spatulated with convergent tips (Fig. 6D).
VARIATION. — The dorsal pelage varies from dark grayish to blackish. In females, the occipital complex may be less distinctly squared due to smaller lambdoidal crests. Sagittal crests in females are also lower and less robust than males, and the nasal process of the premaxilla is less developed. The upper incisors vary among individuals with some specimens being less spatulated and more elongated than average (AMNH 10245).

DISTRIBUTION. — *M. aztecus* is widely distributed from Mexico and Central America (Dolan 1989) to South America, in Venezuela (Handley 1976; Ochoa et al. 1993; Lim & Engstrom 2001) and southeastern Brazil (Gregorin et al. 2011). This study extends the distribution of *M. aztecus* to nine Brazilian states confirming the occurrence of the species in Mamanguape (Paraíba), Huinatá (Amazonas), Rio de Janeiro (Rio de Janeiro), São José do Piauí (Piauí), Corumbá (Mato Grosso do Sul), Crato (Ceará), Lavras and Sete Lagoas (Minas Gerais), Exu (Pernambuco), Salvador (Bahia), and Ilha dos Búzios (São Paulo) (Fig. 7).

REMARKS

The body size of *M. aztecus* is very similar to *M. molossus* and therefore, these two taxa are frequently confused. However, both species are distinguished by several qualitative characters, such as a pale band at the base of the dorsal hair, which is discrete or imperceptible in *M. aztecus*, and long and obvious in *M. molossus*. The dorsal fur of *M. aztecus* is grayish to blackish, while *M. molossus* usually has a cocoa to cinnamon brown colouration. *M. aztecus* has a shorter and inflated braincase and domed skull (Fig. 6C), while in *M. molossus* the skull is more elongated. The sagittal and lambdoidal crests in *M. aztecus* are more developed (Fig. 6B) than in *M. molossus*. In *M. aztecus*, the rostrum is triangular (Fig. 6D), whereas in *M. molossus* it is rectangular. The infraorbital foramen in *M. aztecus* opens laterally (Fig. 6D) while in *M. molossus* it opens frontally. The occipital in *M. aztecus* has a clear quadrangular format (Fig. 6B), while in *M. molossus* this structure is triangular or rounded. The upper incisors in *M. aztecus* are flat and spatulated (Fig. 6D), unlike *M. molossus*, which has elongated and tapered upper incisors with parallel tips. Although some authors do not consider *M. aztecus* as a valid species (Jennings et al. 2000; Eger 2008), our data indicate that it is consistently distinguishable from *M. molossus* and *M. coibensis* based on morphological characters, corroborating Dolan (1989) and Gregorin et al. (2011).

**Molossus coibensis** Allen, 1904

*Molossus coibensis* Allen, 1904: 227.


*Molossus cheriei* Allen, 1916: 35 (type locality: Tapirapoa, Mato Grosso, Brazil).

*Molossus burnsi* – Hershkovitz 1949: 454 (misspelling of *Molossus barnesi* Thomas, 1905).

*Molossus burnsi* *Molossus aztecus lambi* Gardner, 1966: 1 (type locality: 11 km, Northeast of Esquintla, Chiapas, Mexico).

EMENDED DIAGNOSIS. — Smallest species of *Molossus*, usually with dark dorsal hairs varying from cocoa brown to blackish. Monochromatic dorsal hair or, if bicoloured, with a pale brown or grayish short basal band not exceeding one third of the total length. Dorsal hairs from 2.0 to 4.0 mm long. Forearm length averaging 36.9 mm (36.1-37.9) in males and 37.0 mm (34.3-37.5) in females; skull length averages 16.4 mm (15.7-16.9) in males and 15.5 mm (14.9-16.7) in females (Table 1). Relatively massive skull with inflated braincase (Fig. 2B). Infraorbital foramen opens frontally (Fig. 2G). Very shallow or absent basioccipital pits (Figs 2C, 8). Nasal process of the maxilla not protruding over the nasal cavity (Fig. 2A). Mastoid process oriented ventrally in dorsal view (Fig. 2E). Quadrangular occipital complex (Fig. 2F) and upper incisors with convergent tips (Fig. 2H).

VARIATION. — Only a single specimen (UFMG 3350) had grayish dorsal pelage instead of brown, and Gager et al. (2016) recorded cinnamon dorsal fur in specimens from Panama. The basioccipital pits are shallow or absent. Upper incisors can vary from short and
spatulated to slightly elongated, but always have convergent tips (AMNH 217448 and AMNH 217449).

**Distribution.** — *M. coibensis* is widely distributed in Colombia, Peru, Ecuador, Venezuela, and Guyana (Eger 2008). The presence of *M. coibensis* in Brazil was firstly recorded by Dolan (1989) under the name *Molossus cherriei* based on a specimen (holotype) from the state of Mato Grosso, and subsequently extended by Costa et al. (2013) to the state of Pará based on six adults and one juvenile female. In this study records of *M. coibensis* were obtained for Cidade da Barra (Bahia), Belo Horizonte (Minas Gerais), São Luís (Maranhão), São Paulo (São Paulo), and Corumbá (Mato Grosso do Sul) (Fig. 9).

**Remarks**

Our morphological analyses indicate that the differences between *M. barnesi* and *M. coibensis* described by Simmons & Voss (1998) represent intraspecific variation, as suggested by Gregorin et al. (2011) and Catzeflis et al. (2016). Some individuals of *M. barnesi* (e.g. AMNH 26905) have dark dorsal fur with a pale band at the base of the dorsal hairs, not exceeding 1/4 of its length. This pattern of variation also occurs in *M. coibensis*, as described in the account of that species. Both the mesopterygoid canal and the crest between the basisphenoid and basioccipital pits are variable in *M. coibensis* (Gregorin et al. 2011). Simmons & Voss (1998) based on the species distributions available at the time, also suggested that there was a large gap in the distribution of these two species: *M. coibensis* would be present in Central America and northwestern South America while *M. barnesi* would be restricted to French Guiana. However, the extension of the distributional range of *M. coibensis* to eastern South America (Lim & Engstrom 2001) and northern Brazil (Costa et al. 2013), together with the small morphological differences found between these two taxa, support *M. barnesi* as junior synonym of *M. coibensis* (Catzeflis et al. 2016).

**Emended diagnosis.** — Largest species of *Molossus* with a dark dorsal pelage varying from dark brown to blackish (Fig. 10). Monochromatic dorsal hairs or, when dichromatic, with a small pale basal band covering no more than 1/4 of the total length. Dorsal hairs reaching 4.0 mm. Forearm length averaging 50.3 mm in males (47.7-55.2) and 50.0 mm in females (46.7-54.0). Greatest length of skull averaging 22.9 mm (20.8-23.8) in males and 21.3 mm (19.9-22.6) in females (Table 1). Skull with inflated rostrum and elongated braincase (Fig. 11A, C). Mastoid process directed laterally in posterior view and occipital square-shaped with highly developed and inclined lambdoidal crests (Fig. 11B). High sagittal crest, particularly in males (Fig. 11B, D). Infraborital foramen opening laterally in frontal view (Fig. 11D). Basoccipital pits with moderate depth. Triangular rostrum in frontal view (Fig. 11D). Pincer-like upper incisors with converging tips (Fig. 11D).

**Variation.** — The dorsal fur is always very dark, ranging from dark brown to blackish. In some individuals, the entire dorsal hair or just the tips are reddish brown (hence the specific epithet). In females, the sagittal and lambdoidal crests are less robust and the nasal process of the pre-maxilla, although also projecting over the nasal cavity, is less developed than in males.

**Distribution.** — *M. rufus* is widely distributed in South America, occurring from Trinidad to Bolivia, Paraguay, Argentina, and in a large portion of Brazil (Eger 2008) (Fig. 12).

**Remarks**

*M. rufus* resembles *M. pretiosus* in having dark pelage, and similar body and cranial size. However, *M. pretiosus* tends to be smaller (Table 1). *M. rufus* has higher sagittal crest when compared to *M. pretiosus*; the mastoid process in *M. rufus*...
Fig. 10. — *Molossus rufus* (E. Geoffroy, 1805). Photo courtesy of Dr Marco A. R. Mello (https://marcoarmello.wordpress.com).

Fig. 11. — Skull of *Molossus rufus* E. Geoffroy, 1805: A, dorsal view; B, posterior view; C, lateral view; D, frontal view. Scale bar: 1 mm.
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The numbers represent the localities described in Appendix 1.

**Molossus molossus** (Pallas, 1766)


*Vesperilio molossus minor* Kerr, 1792: 97 (type locality Antilles).


*Molossus longicaudatus* E. Geoffroy, 1805: 279 (type locality: not specified).


*Molossus crassicaudatus* E. Geoffroy, 1805: 279 (type locality: not specified).

*Molossus acuticaudatus* Desmarest, 1820: 116 (type locality: Brazil).

*Disopos velox* Temminck, 1826: 234 (type locality: Brazil).

*Molossus maxenii* D’Orbigny, 1835: pl. 11, figs 1-4 (type locality: Moxos, Beni, Bolivia).

*Disopos olivaceo-fuscus* Wagner, 1847: 202 (type locality: Cuiaba, Mato Grosso, Brazil).

*Disopos amplexicaudatus* Wagner, 1847: 203 (type locality: Caicara, Mato Grosso, Brazil).

**Molossus tropidorhynchus** Gray, 1839: 6 (type locality: Cuba).

**Molossus molossus obscurus** — Peters 1866: 575 (name combination).

**Molossus pygmaeus** Miller, 1900: 162 (type locality: Curacao, Antilles).

**Molossus debilis** Miller, 1913: 90 (type locality: Saint Kitts, Antilles).

**Molossus fortis** Miller, 1913: 89 (type locality: Luquillo, Puerto Rico).

**Molossus daintiensis** Allen, 1916: 530 (type locality: Daule, Los Rios, Ecuador, Ceara, Brazil).

**Molossus major crassicaudatus** — Hershkovitz 1949: 454 (name combination).

**Molossus molossus crassicaudatus** — Koopman 1978: 21 (name combination).

**Molossus molossus** — Willig 1985: 671 (misspelling).

**Molossus molosus** — Polanco-Ochoa et al. 2000: 675 (misspelling).

**EMENDED DIAGNOSIS.** — Medium-sized *Molossus* with brown dorsal fur varying from cinnamon to cocoa brown (Fig. 13). Dorsal hairs noticeably bicoloured, with pale basal band reaching ½ to ¾ of total length of the hair. Forearm length averaging 40.2 mm in males (36.2-42.6) and 39.5 mm in females (36.4-42.6). Greatest length of skull averaging 17.7 mm (16.4-18.7) in males and 16.9 mm (15.6-18.6) in females (Table 1). Elongated skull (Fig. 2A) and infraorbital foramen facing anteriorly when observed in frontal view (Fig. 14B). Basiopterygoid pits moderately deep (Fig. 14C) and mastoid process ventrally oriented (Fig. 14D). Triangular or rounded occipital with underdeveloped lambdaid crests (Fig. 14D), and low sagittal crest (Fig. 2B, E). Elongate upper incisors with parallel tips (Fig. 14B). Nasal process of pre-maxilla undeveloped, not protruding over the nasal cavity (Fig. 14E).

**VARIATION.** — Dorsal pelage in *M. molossus* is highly variable, from cinnamon to cocoa brown. Some individuals have a very dark pelage, while others, mostly young specimens, have a grayish fur. The incisor thickness may also vary within series, going from tapered (AMNH 235285) to moderately wide and somewhat spatulated (AMNH 238351).

**DISTRIBUTION.** — *M. molossus* is one of the most widely distributed bat species in the Neotropics, occurring from southeastern United States to Argentina, and throughout the Caribbean islands (López-González & Presley 2001). In Brazil, this species has been recorded from the state of Amazonas to Rio Grande do Sul (Eger 2008). In the present study, we added a new record from Alagoinha, state of Alagoas (Fig. 15).

**REMARKS**

There is a clear morphometric difference between samples of *M. molossus* males from state of Rio Grande do Sul, southern Brazil, and other localities. However, no single qualitative morphological character corroborates the distinction of these samples other than the overall size. Therefore, the difference in size may be an intraspecific variation explained by latitude (Bergmann 1847; Brown 1995; Ashton et al. 2000; Souza 2011). Future studies analyzing genetic divergence should be made to test the hypothesis that these samples are significantly different from each other.
Fig. 13. — Molossus molossus (Pallas, 1766) skull: A, dorsal view; B, frontal view; C, ventral view; D, posterior view; E, lateral view. Scale bar: 1 mm.

Fig. 14. — Molossus molossus (Pallas, 1766). Photo courtesy of Dr Marco A. R. Mello (https://marcoarmello.wordpress.com).
Molossus currentium Thomas, 1901

Molossus obscurus currentium Thomas, 1901: 438 (type locality: Goya, Corrientes, Argentina).

Molossus currentium – Miller 1913: 89 (first use of the current name).

Molossus major currentium – Herschkowitz 1949: 454 (name combination).

Molossus major crassicaudatus – Cabrera 1958: 130 (name combination).


Molossus molossus crassicaudatus – Barquez et al. 1999: 221 (name combination).


Molossus bondae Allen, 1904: 228 (junior synonym of Molossus currentium).

**Distribution.** — In South America *M. currentium* was recorded in Colombia, Ecuador, Venezuela, Argentina, Paraguay, and Brazil (López-González & Presley 2001; Eger 2008). The occurrence of this species in Brazil was first reported based on a juvenile female from Manaus, Amazonia (AMNH 40724) (López-González & Presley 2001). However, the identification of this individual remains uncertain as noted by Eger (2008) and confirmed by us. For this reason, this record is not considered in the present study. Tavares et al. (2010) identified several specimens as *M. currentium* in the state of Minas Gerais. However, these individuals have small cranial and external measurements, the dorsal hairs have an evident pale band at the base, and several cranial features are more similar to *M. molossus* than *M. currentium*. Therefore, these specimens are herein assigned to *M. molossus*. In this paper, an adult male of *M. currentium* from Corumbá, Brazilian state of Mato Grosso do Sul, was recorded (Fig. 17).

**Remarks**

Thomas (1901) described the subspecies *Molossus obscurus currentium* Thomas, 1901 from a series of specimens earlier assigned to *Molossus obscurus* Geoffroy Saint-Hilaire, 1805 from Goya, Corrientes, Argentina. Further analyses considered *M. obscurus obscurus* as a junior synonym of *M. molossus* (Dolan 1989; Freeman 1981) and *M. obscurus currentium* as *Molossus bondae* (López-González & Presley 2001). López-González & Presley (2001) argued that the name *M. bondae* Allen 1904 is a junior synonym, and that the valid name for the species should be *Molossus currentium* Thomas, 1901. However, some authors suggest that *M. currentium* and *M. bondae* should be considered different species. Simmons & Voss (1998) and Eger (2008) argued that the pelage of *M. bondae* is monochromatic or with a short, almost indistinguishable pale band at the base of the dorsal hairs, while in *M. currentium* the dorsal fur is markedly bicoloured with a long whitish basal band. These authors also suggest that the upper incisors of both species are distinct, and *M. bondae* resembles *M. aztecus* and *M. rufus* with pincer-like upper incisors, while *M. currentium* resembles *M. molossus* with elongated and tapered incisors.

In this study, we have analyzed several specimens identified as *M. bondae* including the holotype, and specimens of *M. currentium* from Colombia, Brazil, and Panama. According to our morphological analyses, there are high levels of variation in dorsal pelage colouration as well as upper incisor shape and other cranial and external characters among specimens representing both taxa, with much overlapping. Indeed, the holotype of *M. bondae* (AMNH 23661) has short, brownish dorsal hairs, with a small paler basal band, like several individuals assigned to *M. currentium* (e.g. AMNH 212908, 185000, 184999). In the holotype of *M. bondae*, the incisors have an intermediary shape between pincer-like (as seen in *M. coibensis* and *M. rufus*) and tapered, as observed in some individuals of *M. currentium* (e.g. AMNH 34235 and 34236). In addition, several cranial features, such as opening of the infraorbital foramina and the shape of the occipital complex, are variable in all samples representing *M. currentium* and *M. bondae*. Therefore, we consider *M. bondae* as a junior synonym of *M. currentium*, in agreement with López-González & Presley (2001) and Simmons (2005), and against Eger (2008).
**Molossus pretiosus** Miller, 1902

*Molossus pretiosus* Miller, 1902: 396 (type locality: La Guáirá, Distrito Federal, Venezuela).

**Emended diagnosis.** — Large-sized *Molossus* with dark dorsal pelage from medium brown to blackish, and an absent or narrow, usually grayish, basal band. Short dorsal hairs varying from 2.0 to 4.0 mm. Forearm length averaging 47.5 mm in males (44.6-48.5) and 47.0 mm in females (44.9-49.0). Greatest length of skull averaging 21.4 mm in males (19.8-22.7) and 19.1 mm in females (18.9-20.9). Short and inflated rostrum and domed braincase (Fig. 2B). Infraorbital foramen opening laterally in frontal view (Fig. 2H). Noticeable crest between the basisphenoid and basioccipital pits due to the very deep basisphenoid pits (Fig. 18). Nasal process of the premaxilla not protruding over the nasal cavity (Fig. 2A). Squarish occipital complex due to the large development and inclination of the lambdoidal crests. Quadrangular rostrum in frontal view. Incisors projecting beyond the canines, an intermediate condition when compared to other species of *Molossus*.

**Variation.** — The dorsal fur is dark, ranging from cocoa brown to blackish. Some individuals are orange in the entire dorsal hair or just in the tips (e.g. USNM 102780, 102767, 102768). Individual variation in the upper incisors exist within samples (Nogueira et al. 2008), and although most individuals have the incisors with parallel tips (tapered), others have pincer-like incisors (e.g. ALP 6896, 6875, 6946, 6943).

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**Fig. 16.** — *Molossus currentium* Thomas, 1901 skull: A, dorsal view; B, ventral view; C, posterior view; D, frontal view. Scale bar: 1 mm.
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distribution. — *M. pretiosus* presently has a disjunct distribution, occurring in Nicaragua, Colombia, Venezuela and Guyana (Koopman 1982; Dolan 1989; Eisenberg 1989; Lim & Engstrom 2001); in Brazil, this species was reported from Campo Grande, Mato Grosso do Sul (Gregorin & Taddei 2000), and Jaíba, northern Minas Gerais (Nogueira et al. 2008). These specimens were examined by us and are assigned to *M. pretiosus* (Fig. 19).

**Remarks**

Some studies have showed that there are two large species of *Molossus* in Brazil (Dolan 1989; Jennings et al. 2000; Gregorin & Taddei 2000; Nogueira et al. 2008). This study corroborates with these authors and *M. pretiosus* can be distinguished from *M. rufus* based on qualitative and quantitative traits (see comparisons in *M. rufus* account).

**Discussion**

Prior to our study, evolutionary relationships based on morphological phylogenetic studies have not been explicitly proposed for *Molossus*. However, several authors have suggested phenetical groupings within the genus based on similarity of a few characters (Miller 1913; Freeman 1981; Dolan 1989; Simmons & Voss 1998; López-González & Presley 2001; López-González-Ruiz et al. 2010; Gregorin et al. 2011). Our analysis supports the monophyly of *Molossus* (Fig. 5) based on morphological characters corroborating Ammerman et al. (2012) and Gregorin & Cirranello (2016). Although weakly supported, the phylogeny also clusters *M. coibensis, M. currentium, M. aztecus, M. pretiosus*, and *M. rufus* in one branch, and *M. sinaloae* and *M. molossus* in another. These results differ slightly from the grouping proposed by Dolan (1989), which clustered *M. currentium* with *M. molossus* and *M. sinaloae*. However, the analysis shows weak support for relationships within the genus and other clades within *Molossus* could not be supported.

The phylogeny proposed in this study shows that morphology by itself is not sufficient to resolve the relationships within the genus and many characters demonstrated degrees of homoplasy. The number of palatal streaks, the position of the upper incisors relative to the canines, the position of the opening of the infraorbital foramen, and the shape of the rostrum in rostral view appear at least twice in the evolutionary history of the group. However, different combinations of morphological characters have shown to be reliable for species identification (Dolan 1989; Gager et al. 2016).

Molecular phylogenies of *Molossus* have been proposed (Lindsay & Ammerman 2016; Lim et al. 2017; Loureiro et al. 2018), but genetic data alone also seems not be enough to resolve the relationships within the genus. Gager et al. (2016), based on the mitochondrial CO1 gene and the control region.
D-loop, examined the relationships of *M. molossus*, *M. rufus*, and *M. coibensis* in Panama, and recognized all as valid taxa. However, the resulting phylogenetic tree included numerous polytomies with most nodes having low statistical support (<70%). Lindsey & Ammerman (2016) reconstructed the phylogeny of some species of *Molossus* based on partial CytB sequences. In their study, *Molossus molossus tropidorrhynchus* Gray, 1839 from Cuba formed a divergent monophyletic lineage, but the branches comprising the samples of *M. molossus*, *M. rufus*, and *M. coibensis* had low support. A more recent study by Loureiro et al. (2018) described a new, highly divergent species of *Molossus* from Guyana and Ecuador (*M. fentoni*) based on morphology, mitochondrial and nuclear genes. However, in their phylogeny, the support for the relationships among some terminal taxa, such as *M. rufus*, *M. coibensis*, and *Molossus* sp from Guyana and Venezuela, is very low.

Morphometric variation of some cranial and external measurements are correlated with latitude in at least three species of *Molossus*, corroborating with trends hypothesized by Bergmann (1847), Brown (1995), Ashton et al. (2000), and Saléowski & Watt (2017). However, these variables are not the same among species or between sexes, and perhaps different ecological variables, such as temperature (Bergmann 1847), food availability (Millar & Hickling 1990), prey size (Erlinge 1987), and competition (Damuth 1993) could affect each species differently. For example, Medeiros et al. (2018) noted rapid body dimensions divergence in *Artibeus planirostris* Spix, 1823 linked to anthropogenic alterations of environment. Some individuals of *M. molossus* from southern Brazil have significant larger cranial and external measurements, and further molecular analyses may be required to investigate the possibility of this population being distinct from other *M. molossus*. In addition, a single individual of *Molossus* sp. from the Caatinga of northeastern Brazil was analyzed. However, the combination of characters found in this individual is unique, which suggest that it may be assignable to a new species. Therefore, we emphasize the need for molecular analysis and more field work focusing to collect additional material in order to solve its taxonomic status.

Morphologically, many species within *Molossus* are highly similar and the lack of traditional characters (pelage, skull, and dentition) to distinguish them resulted in an unsatisfactory identification of specimens of this genus. Furthermore, some
characters showed high levels of variation within samples or between sexes, which results in difficulty in the identification and delimitation of species. The level of genetic divergence, even among well characterized species of the genus, is low (Clare et al. 2007; Borisenko et al. 2008; Lim et al. 2017; Loureiro et al. 2018), often making characterization of biologically meaningful subunits difficult, and likely resulting in an underestimation of the actual species richness in the genus. The combination of these factors makes *Molossus* a taxonomic challenge. We suspect that the diversity within *Molossus* is underestimated, and new molecular analyses (e.g., multi-genes, and single nucleotide polymorphism – SNPS) will be important for resolving its relationships. However, morphological analysis are also crucial for the understanding of this complex genus and should be used in combination with other data sets. Echolocation calls have been providing a good dataset to distinguish species of *Molossus* (Jung et al. 2014; Gager et al. 2016; Mischiatto 2018; Aguilar et al. 2018), and it is proven to help deciphering cryptic species complex (Ramasindrazana et al. 2011, Thoisy et al. 2014). Therefore, acoustics could also help to bring information about cryptic species within *Molossus* and understand the taxonomy of the genus. In a recent example, CytoB variation in *M. molossus* as recovered by Lindsey & Ammerman (2016) suggests that two subspecies, *M. m. tropidorchynus* and *M. m. daulensis* Allen, 1916 may be considered as full species, agreeing with previous recorded morphological differences diagnostic of both subspecies. Despite their ubiquitous distribution in Brazil, we have presented a large number of external, cranial, and dental characters, which we expect to be useful for the diagnosis of the six species of *Molossus* identified for the country.

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Kerr R. 1792. — The animal kingdom or zoological system, of the celebrated Sir Charles Linnaeus. Class I. Mammalia:Containing a complete systematic description, arrangement, and nomenclature, of all the known species and varieties of the Mammalia, or animals which give suck to their young; being a translation of that part of the systema naturae, as lately published, with great improvements, by Professor Gmelin of Goettingen. Together with numerous additions from more recent zoological writers, and illustrated with copperplates. Edinburgh, A. Strahan, T. Cadell, and W. Creech, xii+1-32+30. 400 p. https://doi.org/10.5962/bhl.title.57940


Submitted on 28 October 2017; accepted on 11 May 2018; published on 18 September 2018.
We examined a total of 493 specimens, 258 females and 235 males. The material studied is housed in the following institutions: American Museum of Natural History, New York City (AMNH); National Museum of Natural History, Washington DC (USNM); Universidade Estadual Paulista, São José do Rio Preto (DZSRJP); Universidade Federal Rural do Rio de Janeiro, Seropédica (ALP); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); Universidade Federal de Lavras, Lavras (CUFLA); Universidade Federal de Minas Gerais, Belo Horizonte (UFMG); Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ); Universidade Federal do Mato Grosso do Sul, Campo Grande (ZUFMS); Centro de Zoonoses da Cidade de São Paulo, São Paulo (CCZSP); Museu de História Natural da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte (MCN).


*Molossus barnesi*: French Guiana: Cayenne (AMNH 267262, 269105).

*Molossus bonodea*: Colombia: Magdalena: Bondo (AMNH 14922, 14924, 23661), Vale Del Cauca (USNM 83959-483964).

*Molossus coibensis*: Brazil: 1. — Bahia: Cidade da Barra (MZUSP 2672); Maranhão: 2. — Parque Estadual do Bacanga, São Luís, MA (UFMG 3404, 3405); Mato Grosso Do Sul: 3. — Brasilândia (MZUSP 28782, 28689); Minas Gerais: 5. — Belo Horizonte (UFMG 3350), 6. — Três Marias (UFMG 3411); São Paulo: 7. — São Paulo (CCZSP15), Guatemala: Dept. Tutiapa (AMNH 217443-217446, 217448, 217449), Panama: Chagres River (AMNH 173919), CHIRIQUI: Coiba Island (AMNH 18731), Veraguas: Montijo (AMNH 18732, 18733); Canal Zone (USNM 314299, 314300, 317648).
### Appendix 1. — Description of characters used in the phylogenetic analysis.

<table>
<thead>
<tr>
<th>Character</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Facial, pelage, and soft palate</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Size of the forearm</strong></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>Measuring 57-61 mm (0); Average, measuring 49-45 mm (1); Small, less than 45 mm (2).</td>
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<tr>
<td><strong>Banding pattern of dorsal fur</strong></td>
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<tr>
<td>Dorsal fur unicolored</td>
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<tr>
<td>Dorsal fur bicolor</td>
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<td><strong>Form of antitragus</strong></td>
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<tr>
<td>Triangular</td>
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<td><strong>Number of palatal streaks</strong></td>
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<td>Eight</td>
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<td>Nine</td>
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<tr>
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<tr>
<td>Height of metaconule on first and second molars</td>
<td>High (0); Low (1).</td>
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<tr>
<td><strong>Height of metaconule on third molars</strong></td>
<td>Low (0); High (1).</td>
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<td>High (0); Low (1).</td>
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### Appendix 2. — Description of characters used in the phylogenetic analysis.

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</tr>
<tr>
<td><strong>Height of metaconule on fourth molars</strong></td>
<td>High (0); Low (1).</td>
</tr>
</tbody>
</table>

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Diversity of Molossus in Brazil

36. — Reserva Biológica do Tinguá: (6229, 6233, 6238, 6241-6243), 37. — Seropedica, Universidade Rural do Rio de Janeiro (ALP 887); Rio Grande Do Sul: 38. — Quinta (AMNH 235381-235390), 39. — Taím (DZSJR 14565-14570); Roraima: 40. — Ilha de Macará (DZSJR 11493), 41. — Santa Maria do Boiaçu (MZUSP 27897, 27898, 27901, 27902, 27905); São Paulo (MZUSP 21093), 42. — Boracéia (MZUSP 15039), 43. — Catanduva (DZSJR 16456), 44. — Ilha de Búzios (MZUSP 10268, 10271 -10273), 45. — Ribeirão Preto (MZUSP 17597), 46. — Bertioga (MZUSP 26410); Venezuela: (MNRS 23052); Argentina: Corrientes: Goya (MCN286).

**Molossus pretiosus**: Brazil: Mato Grosso Do Sul: 1. — Cumbá (ZUFMS CH100682, CH101360); Minas Gerais: 2. — Jaíba (ALP 6875, 6896, 6911, 6912, 6914, 6915, 6943-6946, 6963); Mexico: Oaxaca: San Blas: (AMNH 14515), Oaxaca: (AMNH 14515); Venezuela: Jupane (AMNH 17037, 17039-17043, 102752, 102754), São Francisco de Cara (USNM 303852), VARGAS: La Guaira (USNM 102744, 102745, 102764-102767), Macuto (USNM 143832-143835, 102767, 102768); Distrito Federal: (USNM 102780).

**Molossus sinaloae**: Honduras: Francisco Morazán (USNM 461105); San Pedro Sula: Chamelecón (USNM 148773). Guatemala: Izabal: Bobos (USNM 260048, 260047). Mexico: Guerrero (USNM 508997, 509001, 508996, 508998); Sinaloa: Escuinapa (AMNH 24524).

**Molossus rufus**: Brazil: Bahia: São Félix do Coribe (CMUFLA 3453).

**Molossus currentium**: Brazil: Manaus (AMNH 17038-17039, 102752), Roraima: Ilha de Macará (DZSJR 11493), 37. — Seropédica, Universidade Rural do Rio de Janeiro (MZUSP 27897, 27898, 27901, 27902, 27905); São Paulo (MZUSP 21093), 42. — Boracéia (MZUSP 15039), 43. — Catanduva (DZSJR 16456), 44. — Ilha de Búzios (MZUSP 10268, 10271 -10273), 45. — Ribeirão Preto (MZUSP 17597), 46. — Bertioga (MZUSP 26410); Venezuela: (MNRS 23052); Argentina: Corrientes: Goya (MCN286).
9. — Upper incisors position relative to vertical plane
Upper incisors project forward in a plane not parallel to the anterior face of canines (0); Aligned to the anterior plan of canines (1). In side view, the incisors may be projected beyond the line of canines (e.g. *Eumops*, *Promops*, and *M. molossus*) (Fig. 2A) or in the same line of canines (e.g. *M. rufus* and *M. aztecus*) (Fig. 2B).

10. — Orientation of the upper incisors
Upper incisors tips divergent (0); Upper incisors tips convergent (1); Upper incisors tips directed ventrally (2). The tips of the upper incisors are divergent in *Eumops* and *Promops*. In contrast, the upper incisors are directed medially in some species of *Molossus* (*M. rufus* and *M. aztecus*) (Fig. 2H) and parallels in other (*M. molossus* and *M. sinaloae*) (Fig. 2G).

11. — Number of upper premolars
Two (0); One (1). *Eumops* and *Promops* present two premolars on each hemimaxilla while *Molossus* has one (Fig. 2C, D).

12. — Size of the third lower premolar
Large and developed, greater than half of the fourth inferior premolar (0); Median size, measuring about half of the fourth premolar (1); Small and undeveloped, with less than half of the length of the fourth premolar (2). In *Eumops* the third premolar is large and developed and in *Promops* it is of median size. In *Molossus* the third premolar is undeveloped, not having more than half the size of the fourth inferior premolar.

13. — Development of metaconid of the third and fourth lower premolars
Undeveloped, not forming projections (0); Well-developed, forming a distinct cusp (1). In *Eumops* the metaconid of the third and fourth premolars is undeveloped. In contrast, in *Molossus* there is a large and developed metaconid forming a distinct cusp.

14. — Presence of hypoconulid in the first lower molar
Present (0); Absent (1). The hypoconulid of the first molar is present in *Eumops auripendulus* and absent in *Molossus*.

15. — Number of lower incisors
Two (0); One (1). *Eumops* and *Promops* have two incisors in each hemimandible. In contrast, *Molossus* has only one.

16. — Development of the entoconid on first lower molar
Developed forming a lateral projection (0); Reduced, not forming a lateral projection (1). The entoconid in *Eumops* is large and developed creating a side projection, while *Molossus* and *Promops* have this crest weak and barely noticeable.

17. — Size of entoconid on the lower third molar
Small and poorly developed (0); Large and developed projecting distally (1). The entoconid on the lower third molar in *Eumops* and *Promops* is small and barely noticeable, while in species of *Molossus* is large and developed forming a lateral projection.

18. — Opisthocranium in posterior view
Straight (0); Curved dorsally and anteriorly (1). In *Eumops* the occipital in posterior view is straight and flat, while in *Molossus* it is curved, which gives the appearance of a dome.

19. — Palate arching
Palate moderately arched. The distance between midline of the palate and the toothrow is about the size of the first molar (0); Palate strongly arched. The distance between the midline of the palate and toothrow is greater than the size of the first molar (1). Palate slightly arched without significant space between the center of the palate and toothrow (2); The hard palate is a complex association of the palatal process of the premaxilla, maxilla, and horizontal process of the palatine bone. In Microchiroptera, the arching palate can range from straight to strongly curved, depending on the diet. In the case of *Promops*, *Eumops*, and *Molossus* this arching decreases, respectively, with *P. centralis* having the most arched palate.

20. — Posterior border of hard palate
V-shaped, with the anterior end tapered (0); U-shaped, with rounded anterior end (1). *Eumops auripendulus* has the V-shaped palate, while *P. centralis* and *Molossus* (Fig. 2C and D) have an U shaped palate.

21. — Shape of the basisphenoid pits
Basisphenoid pits long and oval (0); Basisphenoid pits circular (1). In *E. auripendulus*, the basisphenoid pits are elongated and oval compared to the genus *Molossus* (Fig. 2D).

22. — Relative width of zygomatic arch along its length
Zygomatic arch with gentle decrease in width along the length (0); Zygomatic arch with a sudden decrease in width along the length (1). The transition from the jugal to squamosal can be abrupt or smooth, making the width of the zygomatic arch along its length homogeneous or variable. In the outgroup taxa there is a gentle decrease in this thickness along its length, while in *Molossus* there is a sudden decrease in this width, forming a process near to the process of the maxilla (Fig. 2A, B).

23. — Depth of basicoclear fissure
Wide (0); Shallow (1). The basicoclear fissure separates the complex of the tympanic bulla from the palatal portion formed by basisphenoid and basioccipital plates. This structure is remarkably deep in *Eumops* and *Promops*, while in *Molossus* it is shallow. The shallow state of this character implies in a contact zone between the bulla and other parts of the skull (Gregorin, 2009).

24. — Number of incisive foramina
One (0); Two (1). *Eumops* and *Promops* have only one incisor foramen while the species of *Molossus* have two.
25. — Size of the sphen-orbital process
Sphen-orbital process small and truncated (0); Sphen-orbital process large, long and tapered (1). The sphen-orbital process is small and truncated in Eumops and Promops and very thin and elongated in Molossus.

26. — Position of the optical channel
Anterior part of the optical channel located at the level of the third molar (0); Anterior part of the optical channel located at the level of the toothrow end (1). In Eumops the posterior part of the optic canal extends to the height of the third molar, while in Promops and Molossus this structure reaches only the end of the dental series (Fig. 2A, B).

27. — Length of the rostrum
Long compared to the braincase (0); Short compared to the braincase (1). Eumops has a proportionately more elongate rostrum, while Promops and Molossus have this region more shortened (Fig. 2A, B).

28. — Basisphenoid pits depth
Basisphenoid pits deep (0); Basisphenoid pits shallow (1); In Molossus and Promops the basisphenoid pits are relatively shallow when compared to E. auripendulus.

29. — Basiooccipital pits depth
Shallow (0); Moderate (1); Deep (2). Within species of Molossus, the depth of the basiooccipital pit varies considerably. In M. coibensis the pits are extremely shallow (Fig. 2C), while in M. pretiosus they are quite deep. Other species of the genus have cavities with moderate depth (Fig. 2D).

30. — Position of the opening of the infra-orbital foramen
Opening of the infra-orbital foramen forward directed (0); Opening of the infra-orbital foramen directed laterally (1). In front view, the skull of some species of Molossus, as M. aztecus and M. rufus (Fig. 2H), show the infra-orbital foramen laterally directed, whereas in other species, such as M. molossus, it opens frontally (Fig. 2G).

31. — Height of braincase
In the same plane as the dorsal region of the rostrum (0); Above the dorsal surface of the rostrum (1); The braincase may be less developed and in the same plane as the dorsal region of the rostrum, giving a flattened appearance to the skull (E. auripendulus), or it may be well developed, extending above the dorsal surface of the rostrum, which gives the appearance of a globose skull (Molossus).

32. — Presence of the crest between the basisphenoid and basiooccipital pits
Absent (0); Present (1). Due to the deepening of basisphenoid and basiooccipital pits, a crest is formed between these cavities in Molossus pretiosus.

33. — Projection of the nasal process of premaxilla
The nasal process of premaxilla does not project over the nasal cavity (0); The nasal process of premaxilla project over the nasal cavity (1). In some species of the genus Molossus such as M. aztecus and M. rufus, the nasal process of the premaxilla is well developed and it is projected over the nasal cavity (Fig. 2B). In other species, such as M. molossus, this structure is less developed not projecting over the nasal cavity (Fig. 2A).

34. — Format of the rostrum in rostral view
Square, with a uniform width along its length (0); Triangular with the width of the dorsal portion narrow (1). In front view, the skull of some species have a quadrangular nasal aperture, as in the case of M. coibensis and M. molossus (Fig. 2G). In other species, such as M. aztecus, the shape of the nasal aperture is triangular, giving the appearance of a slender rostrum (Fig. 2H).

35. — Robustness of the skull
Slender and elongated skull (0); Robust skull (1). In M. molossus the skull is elongated with an elongated braincase and an inflated rostrum, giving it a slender look. In M. coibensis and M. aztecus, the braincase is more globular and they have a more inflated rostrum, giving it a more robust appearance.

36. — Development of medial sagittal crest in males
Absent (0); Undeveloped (1); Well developed (2). Eumops auripendulus do not have a sagittal crest, while Molossus species have it with variable sizes. In some species such as M. coibensis, M. aztecus, and M. rufus, the sagittal crest is well developed Fig. 2B, F and H), while in other species such as M. molossus the crest is less developed when compared with the size of the skull (Fig. 2A, E, G).

37. — Development of lambdoidal crest in males
Low (0); Very high (1). In Eumops, Promops and in some species of Molossus, such as M. molossus and M. sinaloae, the lambdoidal crest is poorly developed (Fig. 2E), whereas in M. aztecus, M. currentium, and M. rufus the crest is high and detached from the occipital (Fig. 2F).

38. — Shape of occipital complex in dorsal view
Triangular (0); Quadrangular (1). Eumops auripendulus, P. centralis, and some species of Molossus, such as M. molossus and M. sinaloae (Fig. 2E), have a triangular or rounded occipital, whereas other species of Molossus have an occipital more robust and quadrangular (Fig. 2F).

39. — Projecting of mastoid process
Paroccipital process projects laterally (0); Paraoccipital process projects frontally (1). The paraoccipital process in E. auripendulus, P. centralis, Molossus sp., and M. rufus projects laterally and can be easily visualized in dorsal view (Fig. 2F). In contrast, in other species of Molossus, the paraoccipital process projects ventrally (Fig. 2E).
APPENDIX 2. — Morphological character matrix used in the phylogenetic analysis. “?” denotes missing data.

| Taxon/Character | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 |
| E. auripendulus | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| P. centralis    | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| M. coibensis    | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| M. molossus     | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| M. aztecs       | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 1 |
| M. currentium   | 2 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 1 |
| M. sinaloae     | 2 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| M. pretiosus    | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 1 |
| M. rufus        | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 1 |
| Molossus sp.    | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | ? | ? | 1 | 0 |